Revision of the genus *Pilsbryna* (Gastropoda: Pulmonata: Gastrodontidae) and comments on the taxonomic status of *Pilsbryna tridens* Morrison, 1935

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ABSTRACT

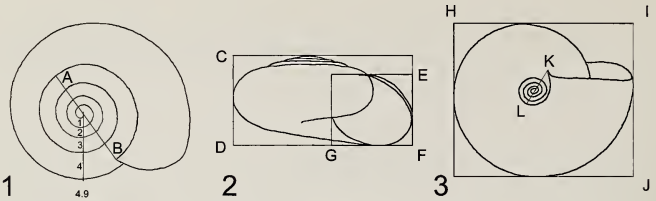
Pilsbryna is revised based on new material collected during recent surveys of wet leaf-litter microhabitats in the southern Appalachian Mountains. Five species are recognized including *Pilsbryna aurea* Baker, 1929, *P. castanea* Baker, 1931, *P. nodopalna* new species and *P. quadrilamellata* new species. All species are redescribed or described. *Pilsbryna vanattai* (Walker and Pilsbry, 1902) is transferred to *Pilsbryna* from *Glyphyalinia* (*Glyphyalus*) based on genital and juvenile shell anatomy. *Pilsbryna tridens* Morrison, 1935, is reexamined based on newly available material; its placement in the genus *Helicodiscus* sensu lato is supported by new radular evidence. *Pilsbryna* species share unique genital and shell characteristics that are included in a redescription of the genus. The new generic definition combined with habitat information for all *Pilsbryna* species allows a better understanding of the geographic and microhabitat distribution of the genus.

INTRODUCTION

Although the terrestrial invertebrate fauna of eastern North America is among the best known in the world, new species are discovered frequently. Most are small species from patchily distributed and poorly sampled microhabitats. Recent collecting in one such habitat, damp to wet leaf-litter surrounding mountain seeps, springs and streams, has uncovered a remarkable radiation of small terrestrial snails of the genus *Pilsbryna*. In this paper, we redescribe the genus, describe two new species of *Pilsbryna*, and redescribe the other three species in the genus including a species formerly placed in the genus *Glyphyalinia*. One other previously described species, *P. tridens*, was reassigned to *Helicodiscus* by Hubricht (1964) without explanation. This generic placement was used in most subsequent publications listing the species (Riedel, 1980; Hubricht, 1985; Turgeon et al., 1988, 1998) although it has remained unconfirmed until now. Newly collected material of *H. tridens* allows for its unequivocal generic assignment.

MATERIALS AND METHODS

Specimens were hand-collected from the leaf-litter/soil interface or sifted from samples of leaf-litter. Live collected animals were narcotized overnight in a suspension of water containing a 1 cm length of mentholated cigarette and then preserved in 75% ethanol. Gross anatomical dissections were made under 75% ethanol using a dissecting microscope. Isolated reproductive systems were stained with Harris haematoxylin and Semichon aceto-carmine stain and cleared with glycerin. Radulae were isolated from dissected buccal masses using a saturated KOH solution. Scanning electron micrographs of shells and radulae were made using a field emission-SEM. Drawings of the shell and genital anatomy were made with the assistance of a camera lucida, and measurements were taken using an ocular micrometer. All line drawings of the internal structures of juvenile shells are in basal view and use solid lines for shell outlines and internal structures that make contact with the inner surface of the translucent base of the shell. Dotted lines indicate structures that are viewed through the translucent base of the shell but do not make contact with the base. Shell measures were made as follows. Whorl count (W) was measured from the suture of the first whorl to the body whorl (Figure 1) and fractions of a whorl were determined with the aid of a cardboard circle divided into 10 equal parts of 36°. Spire diameter (SD) was measured as the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture (Figure 1, line a–b). Height (H) was the greatest distance between the apex and the base of the aperture measured parallel to the shell axis (Figure 2, line c–d). Aperture height (AH) was measured from the suture to the base of the aperture, parallel to the shell axis (Figure 2, line e–f). Aperture width (AW) was the greatest distance from the apertural edge of the umbilicus to the outer edge of the aperture (Figure 2, line g–f). Greater diameter (GD) was the measure of the greatest width of the shell (Figure 3, line h–i), and lesser diameter (LD) was the diameter perpendicular to



Figures 1–3. Shell measurements: **1.** Whorl count (1–4.9), spire width (line A–B). **2.** Shell height (line C–D), aperture height (line E–F), aperture width (line F–G). **3.** Greater diameter (line H–I), lesser diameter (line I–J), umbilical width (line K–L).

the greater diameter (Figure 3, line i–j). Umbilical Width (UW) was measured from the inner edge of the aperture through the center of the umbilicus to the opposite side of the umbilicus (Figure 3, line k–l). Maps were made with the assistance of DeLorme, Topo USA software. We examined specimens of *Pilsbryna* in the collections of the Academy of Natural Sciences, Philadelphia (ANSP), Field Museum of Natural History, Chicago (FMNH), North Carolina State Museum, Raleigh (NCSM), National Museum of Natural History (USNM) and Florida Museum of Natural History, Gainesville (UF) and the private collection of one of the authors (BC).

The following abbreviations are used in figures of genital anatomy: AG = albumen gland, EP = epiphallus, HD = hermaphroditic duct, OV = free oviduct, PE = penis, PG = prostate gland, PP = penial papillae, PR = penial retractor muscle, SD = spermathecal duct, SP = spermatheca, UT = uterus, VD = vas deferens. Anatomical terminology follows Pilsbry (1946); for alternate usages see Tompa (1984).

SYSTEMATICS

Family Gastrodontidae Tryon, 1866
Genus *Pilsbryna* Baker, 1929

Type Species: *Pilsbryna aurea* Baker, 1929 by monotypy.

Description: Small snails of the family Gastrodontidae with depressed-helicoid and umbilicate shells of roughly 5 whorls that are sculptured with closely placed, shallow axial grooves. Whorl expansion is slow and regular through the penultimate whorl and more rapid in the body whorl. Shells of juveniles usually contain spirally arranged lamellae or nodules within the shell. These lamellae or nodules occur at mid parietal and various other positions from columellar to sutural, and are reduced or completely resorbed in adult shells.

The apical ⅓ to ½ of the penis bears papillae that are not located within a well-defined apical chamber. The base of the penis is thin-walled and simple. The penial retractor muscle is inserted near the apex of the penis. The epiphallus is robust, of similar diameter to the penis, does not bear a caecum and joins the penis laterally at the apex. The epiphallus is well defined at the junction with the vas deferens. The spermathecal duct is long and slender and the spermatheca ovate. There are no well-defined glandular areas within the free oviduct.

The form of the radula is typical of many small North American Gastrodontidae. The centrals are symmetric and tricuspid and of similar height to the first laterals. There are three asymmetric tricuspid laterals on each side of the central, and numerous unicuspid marginals.

Remarks: *Pilsbryna* has been treated as a subgenus of *Paravitrea* by Riedel (1980); however, similarities between the two genera are superficial or shared by several other groups of North American Gastrodontidae. Although both *Pilsbryna* and *Paravitrea* possess internal barriers in the shell, the form and position of these barriers differs. Juvenile *Pilsbryna* possess spiral lamellae or series of nodules, usually at the parietal, palatal and basal positions. *Paravitrea* species usually have axial rows of two to many, evenly spaced, small lamellae grouped ¼ to ⅓ whorl apart that are not concentrated near the aperture. The shells of *Paravitrea* are more tightly coiled, usually with 6 or more whorls while shells of *Pilsbryna* attain fewer than 6 whorls and more closely resemble those of some *Glyphyalinia* and *Nesovitrea*. Analysis of genital characters also does not support the placement of *Pilsbryna* within the genus *Paravitrea*. The genital anatomy of all known species of *Pilsbryna* is highly conserved and the combination of genital characters found in *Pilsbryna* are not found in *Paravitrea* or in any other group of North American Gastrodontidae. Similarities in radular anatomy between *Pilsbryna* and *Paravitrea* are not unique; they are shared with most small American Gastrodontidae, including *Glyphyalinia* and *Nesovitrea*. The unique apertural barriers of the shell, the rows of papillae at the apex of the penis and the unusual habitat shared by *Pilsbryna* species strongly suggest the group is monophyletic and distinct from other genera of small American Gastrodontidae. In any case, evidence of a particularly close relationship between *Pilsbryna* and *Paravitrea* is lacking, and *Pilsbryna* is here considered a distinct genus.

Pilsbryna aurea Baker, 1929
Common name: ornate bud
(Figures 4–10, Table 1)

Pilsbryna aurea Baker, 1929a: 91–92, pl. 3, figs. 4–8; Baker, 1929b: 260–261, pl. 9, figs. 4–5; Baker, 1931: 112–113, pl. 19, figs. 9–13, pl. 20, fig. 5; Pilsbry, 1946: 389–391, fig. 205(4–5), fig. 206(a–c), fig. 207(9–13), fig. 208(5); Baker, 1962: 3; Burch, 1962: 107, fig. 257; Hubricht, 1973: 14; Turgeon et al., 1988: 135; Turgeon et al., 1998: 148.

Diagnosis: A medium-sized *Pilsbryna* with an adult shell diameter of 2.9–3.6 mm, height of 1.4–1.9 mm and 5.0–5.4 whorls. Shells of less than 3.5 whorls contain two lamellae, one crescent-shaped at mid-columellar position, the second blade-shaped or undulate at mid-parietal position. Both lamellae extend up to ⅓ whorl into the body whorl. The parietal lamella is often thickened along its distal edge giving it a T-shaped cross section.

Description: Shell depressed-helicoid, umbilicate, glossy, translucent and densely sculptured with irregularly spaced, indented axial lines (Figures 4–6). Adult shell (Table 1) about 2.9–3.6 mm (mean = 3.2, n = 10) in major diameter and 1.4–1.9 mm (mean = 1.7) in height with 5.0–5.4 (mean = 5.1) slowly expanding whorls. The shell height/greater diameter ratio is 0.48–0.56 (mean = 0.52) and the spire width/greater diameter ratio is 0.53–0.60 (mean = 0.57). The final ⅓ of the body whorl expands slightly more rapidly than previous whorls; the lesser/greater diameter ratio is 0.82–0.91 (mean = 0.86). The aperture is ovate, widest at or slightly below the middle of the whorl. The umbilicus is 0.4–0.6 mm (mean = 0.5) in diameter and 0.13–0.19 (mean = 0.16) of the greater diameter of the shell. The funnel shaped umbilicus expands regularly until the final third of the body whorl, where it expands more rapidly. Shells of immature animals contain two lamellae, a crescent shaped lamella at mid-columellar position and an undulating lamella at mid-parietal position (Figures 7–8). Both lamellae extend up to ⅓ whorl into the aperture. The parietal lamella is usually thickest distally and is often T shaped in cross section. Both lamellae are much reduced and more often completely resorbed in adults.

The basal half of the penis is straight-sided and simple while the apical half is robust, bearing numerous small papillae (Figure 9). The penial retractor muscle is subapically inserted. The epiphallus is about the same length and roughly half the diameter of the penis and inserts laterally at the apex of the penis. The diameter of the epiphallus remains roughly constant and widens only slightly at the junction with the narrow vas deferens. The epiphallus is folded at the mid-point and also has longitudinal folds internally. The spermatheca is ovate, and the narrow spermathecal duct expands very slightly basally. The free oviduct is roughly twice the diameter of the base of the penis, expanding slightly at the junction with the spermathecal duct. A caecoid outpocketing was not observed on the free oviducts of two dissected adults.

The central tooth of the radula is symmetrically tricuspid; the mesocone is slender, especially basally, expanding slightly above the ectocone cusps and then tapers slowly to the apex (Figure 10). The ectocones are short, roughly ⅓ the total height of the tooth, symmetrical and diamond-shaped. The three laterals are tall, slender, and asymmetrically tricuspid. The endocone is tall about ⅔ the height of the mesocone. The ectocone is ⅓ the height of the mesocone and separated from it by a narrow gap. The marginals are tall, slender and unicuspid, with concave peripheral edges and convex proximal edges. We studied two radulae (UF 287063) using SEM microscopy. Both had twenty marginals on each side.

Holotype: ANSP 147189a. Baker (1929a) figured and measured this shell and designated it as the type, thereby fixing the holotype.

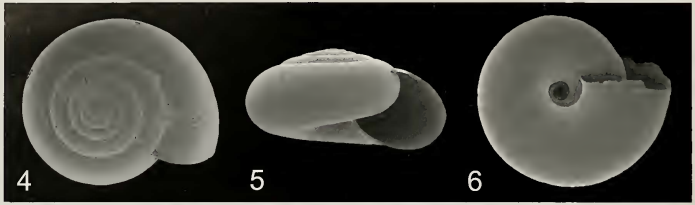
Paratypes: ANSP 147189, type locality, Baker, 1928.

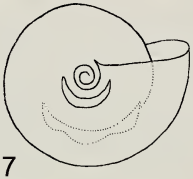
Type Locality: USA, Tennessee, Unicoi County, Limestone Cove, Big Springs, between Unaka and Stone Mountains, about 11 km E of Unicoi, 36° 11′ N, 82° 17′ W, elevation 700 m, Baker, 1928.

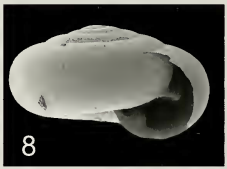
Other Material Examined: ANSP 158890, USA, Tennessee, Unicoi County: Limestone Cove; ANSP 152469, type locality, Baker, 1928; ANSP 165583, Baker, 26–30 Aug. 1928; UF 292089, UF 287063, Davis Springs, 8 km E of Unicoi, 36°10.7′ N, 82°16.4′ W, 687 m elevation, J. Slapcinsky and B. Coles, 31 May 2001; FMNH 248868, near Davis Springs, 8 km E of Unicoi, L. Hubricht, 18 May 1961; FMNH 248867, 2.1 km SE of Limestone Cove, L. Hubricht, 28 May 1974; BC 6761, Washington County, Dry Creek Road, 1 km S of Jim McNeese Road, 36° 15.6′ N, 82° 21.9′ W, 637 m elevation, B. Coles, 21 May 2002.

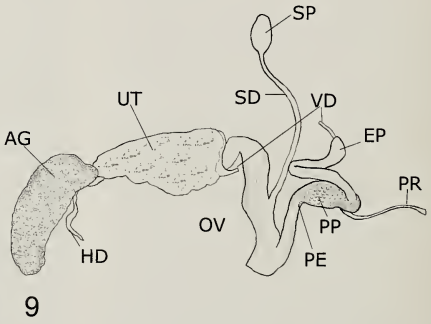
Remarks: Several characters of the genital and radular anatomy differed from previously published descriptions. A caecoid outpocketing was not observed on the free oviducts of two adults dissected in this study; in contrast, Baker (1929b) recorded it in a juvenile. However, reproductive structures, especially those of the posterior portion of the reproductive system, can vary in size, shape, color and texture with maturation and reproductive stage (Emberton, 1985). Our observations of the structures of the anterior portion of the reproductive system compare well with those of Baker (1929b). This study using SEM microscopy found twenty marginals per side. In contrast, Baker (1929b), using light microscopy, recorded only 14 marginals in an immature specimen.

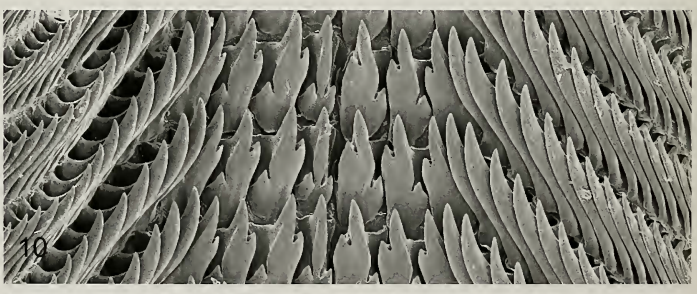
Pilsbryna aurea appears most similar to *Pilsbryna quadrilamellata* described below, juvenile shells of these two share unique crescent-shaped columellar lamellae and lack spiral rows of nodules at any position. However, the two species are easily separated using other juvenile shell characters: *P. aurea* has a distally expanded parietal lamella and does not possess the mid-basal and sutural lamellae of *P. quadrilamellata*. Anatomically, *P. aurea* can











Figures 4–10. *Pilsbryna aurea.* **4–6.** UF 287063, diameter 3.2 mm. **7.** FMNH 248868, diameter 2.6 mm. **8.** UF 287063, diameter 2.1 mm. **9.** Camera lucida drawings of genitalia, UF 292089, maximum width 5.9 mm; **10.** UF 292089, horizontal field width = 217 μm.

Table 1. Measurements in mm of undamaged adult shells of five species of *Pilsbryna*, N = 10. GD = greater diameter, LD = lesser diameter, H = height, AW = aperture width, AH = aperture height, SW = spire width, UW = umbilicus width, W = number of whorls.

		GD	LD	H	AW	AH	SW	UW	W
P. aurea	Mean ± SD	3.2 ± 0.2	2.8 ± 0.2	1.7 ± 0.2	1.5 ± 0.1	1.3 ± 0.1	1.8 ± 0.1	0.5 ± 0.1	5.1 ± 0.1
	Range	2.9–3.6	2.5–3.0	1.4–1.9	1.3–1.7	1.2–1.4	1.7–2.0	0.4–0.6	5.0–5.4
P. castanea	Mean ± SD	3.7 ± 0.2	3.2 ± 0.1	2.0 ± 0.1	1.7 ± 0.1	1.5 ± 0.1	2.1 ± 0.1	0.7 ± 0.1	5.2 ± 0.2
	Range	3.5–3.9	3.0–3.4	1.9–2.2	1.6–1.8	1.4–1.6	2.0–2.3	0.6–0.8	5.0–5.4
P. nodopalma	Mean ± SD	3.0 ± 0.1	2.6 ± 0.1	1.5 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.7 ± 0.1	0.5 ± 0.1	4.5 ± 0.1
	Range	2.7–3.1	2.4–2.8	1.4–1.6	1.3–1.5	1.2–1.3	1.6–1.8	0.4–0.5	4.3–4.6
P. quadrilamellata	Mean ± SD	3.2 ± 0.2	2.8 ± 0.2	1.7 ± 0.1	1.5 ± 0.1	1.3 ± 0.0	1.9 ± 0.1	0.5 ± 0.1	5.0 ± 0.2
	Range	2.8–3.4	2.5–3.0	1.5–1.8	1.4–1.6	1.3–1.4	1.8–2.2	0.4–0.6	4.7–5.2
P. vanattai	Mean ± SD	4.0 ± 0.2	3.4 ± 0.2	2.0 ± 0.1	2.0 ± 0.2	1.7 ± 0.1	2.0 ± 0.1	0.5 ± 0.1	4.8 ± 0.2
	Range	3.8–4.4	3.2–3.7	1.9–2.2	1.8–2.3	1.5–1.9	1.9–2.3	0.5–0.6	4.6–5.1

be distinguished from other species of *Pilsbryna* by the unusually inflated apex of its penis and by the clearly subapical insertion of its penial retractor muscle. The teeth of the radula are tall and slender. The central tooth is especially slender, and unlike other *Pilsbryna* species, does not bear a strong angle at its widest point. The peripheral ectocones are relatively poorly defined, separated from the adjacent mesocone by narrow gaps similar to those of *P. castanea* and *P. nodopalma*, described below, and unlike those of *P. quadrilamellata* and *P. vanattai*.

Habitat and Distribution: Previously, *Pilsbryna aurea* was known from sites within 3 km of the town of Limestone Cove in Unicoi County, Tennessee (Baker, 1929a; Hubricht, 1973). Recent collecting has also uncovered this species along Dry Creek Road, south of Johnson City, a range extension of more than 10 km to the northwest. This species appears to be restricted to mountain valleys near Unicoi, Tennessee, and has been found at elevations of 600–700 m. Known populations occur on rocky wooded hillsides along small streams. The species is most common in wet leaf-litter along streams and around seeps but is also found in deep leaf-litter at the base of limestone and other sedimentary rocks along stream banks.

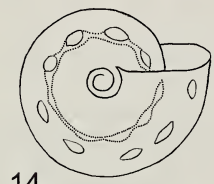
Pilsbryna castanea Baker, 1931
Common name: prominent bud
(Figures 11–17, Table 1)

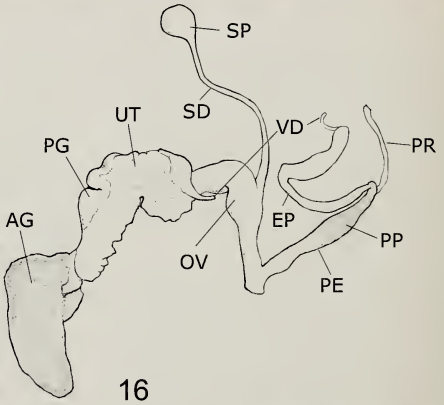
Pilsbryna castanea Baker, 1931: 111–112, pl. 19, figs. 1–8, pl. 20, fig. 4; Pilsbry, 1946: 391–393, fig. 207(1–8), fig. 208(4); Baker, 1962: 5; Burch, 1962: 94, 98, 106, fig. 219, fig. 228, fig. 256; Hubricht, 1973: 14; Turgeon et al., 1988: 135; Turgeon et al., 1998: 148.

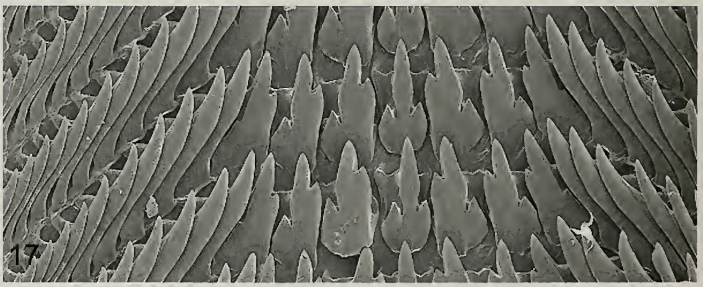
Diagnosis: A medium to large *Pilsbryna* with an adult shell diameter of 3.4–3.9 mm, height of 1.9–2.2 mm, and whorl count of 5.1–5.4 whorls. Shells with fewer than 4 whorls have a sinuous parietal lamella and a spiral series of basal nodules extending a full whorl into the aperture. Shells 4.5 whorls contain only a few basal nodules roughly half way into the body whorl and all traces of lamellae are resorbed in most adults.

Description: The shell is depressed-helicoid and umbilicate, with its surface sculptured with dense and irregularly spaced axial indentations (Figures 11–13). *Pilsbryna castanea* is relatively high-spired (Table 1), with a shell height of 1.9–2.2 mm (mean = 2.0, n = 10), width of 3.4–3.9 mm (mean = 3.7) and height/width ratio of 0.51–0.58 (mean = 0.55). The shell is relatively tightly coiled with 5.1–5.4 (mean = 5.2) whorls; the final ⅓ of the body whorl expands slightly more rapidly than previous whorls and the ratio of lesser/greater diameter is 0.82–0.89 (mean = 0.86). The spire is 0.55–0.61 (mean = 0.58) of the greater diameter. The umbilicus is relatively straight-sided and 0.6–0.8 mm (mean = 0.7) wide; the ratio of umbilical width/greater diameter is 0.17–0.21 (mean = 0.19). Juvenile shells with fewer than four whorls usually have a mid-parietal lamella and a spiral row of low nodules at basal position (Figures 14–15). Both often extend a full whorl or more into the aperture. The position of the basal nodules coincides with the summits of the undulating parietal lamella. Animals with shells more than four whorls gradually stop producing lamellae and begin to resorb previously deposited lamellae. The shells of animals approaching maturity often contain traces of the lamellae a half whorl into the aperture; by the time most animals reach maturity all traces of apertural barriers are resorbed.

The penis is narrow and elongate, slightly constricted above the base, expanding slowly apically, widest ⅔ from the base, then tapering slowly to the apex (Figure 16). The apical half bears small papillae. The penial retractor muscle is inserted nearly apically. The epiphallus is longer than the penis, and joins it laterally at the apex. The epiphallus is narrowest near the junction with the penis is folded at mid-point, and slightly inflated towards the vas deferens. The vas deferens is narrow; the junction with the much wider epiphallus is well defined. Free oviduct is slightly wider than the penis, where they meet and widens at and above the attachment of the sper-







Figures 11–17. *Pilsbryna castanea.* **11–13.** UF 297381, diameter 3.6 mm. **14.** UF 297381, diameter 2.6 mm. **15.** UF 297381, diameter 2.4 mm. **16.** Camera lucida drawings of genitalia, UF 297419, maximum width 5.8 mm. **17.** UF 297419, horizontal field width 205 μm.

mathecal duct. Spermathecal duct is long and narrow; the spermatheca is ovate. One animal was dissected.

The central tooth of the radula is tall, slender and tricuspid (Figure 17). The mesocone is elongate, widest and angular slightly above the ectocone cusps and tapering sharply towards the apex and narrowing towards the base. The ectocones are slightly less than ½ the total height of the tooth, symmetrical, and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocone of each is tall and the ectocone short. The seventeen marginal teeth on each side are tall, slender and unicuspid, with concave peripheral, and convex proximal, edges. One radula was examined.

Holotype: ANSP 152468a. Baker (1931) figured and measured this shell and designated it the type, thereby fixing the holotype.

Paratypes: ANSP 152468, type locality.

Type Locality: USA, Tennessee, Marion County, Dove, mouth of Cave Cove, west facing hillside south of big spring, which forms eastern source of Battle Creek, 35°10′ N, 85°47′ W, 244 m elevation, Baker, 1931.

Other Material Examined: ANSP 165582, USA, Tennessee: Marion County, type locality, Baker, 23–26 Jul. 1928; FMNH 171387, west side of Battle Creek at junction of Ladd's Cove Road and Interstate 24, 35°8.7′ N, 85°46.7′ W, 193 m elevation, 4 Sep. 1974, G. Goodfriend; UF 297419, UF 297381, 9 Jun. 2002, J. Slapcinsky; FMNH 171403, Martin Springs 10 km south of Monteagle, 4 Sep. 1974, G. Goodfriend; FMNH 248870, 8 km N of Sequatchie, near large spring, 23 Oct. 1962, L. Hubricht; UF 306530, Bledsoe County, Lusk Loop Road, 0.5 km NW of Cannon Creek, 35°30.1′ N, 85°18.9′ W, 300 m elevation, 1 Jun. 2003, J. Slapcinsky; FMNH 171335, NE side of Rains Gulf, 18 km SW of Pikeville, 410 m elevation, 7 Sep. 1974, G. Goodfriend; ANSP 165581, Cannon Creek, W of Pikeville, 1928, H. B. Baker.

Remarks: Like *Pilsbryna nodopalma*, described below, and *P. vanattai*, juvenile *P. castanea* have spiral series of nodules. *Pilsbryna castanea* can be distinguished from the other two species because it does not possess a second series of nodules at the palatal position. The nodules are peg-shaped and not dorsoventrally compressed like those of *P. nodopalma*. The nodules in *P. castanea* can extend the entire body whorl, much farther than those of the other nodulate species. However, this last character is less useful when comparing older juveniles that have discontinued deposition of lamellae and have begun to resorb previously deposited barriers. The adult shells of *P. castanea* are larger than those of *P. nodopalma*, have a greater height/width ratio than *P. vanattai*, and have more whorls than either species.

Habitat and Distribution: *Pilsbryna castanea* is found on wooded hillsides bordering Battle Creek and the Sequatchie Valley in Marion and Bledsoe Counties, Tennessee (H.B. Baker, 1931; Pilsbry, 1948; Hubricht, 1973, 1985). All animals were found in deep leaf-litter at the base of limestone exposures. Live specimens are most common in wet leaf-litter surrounding seeps.

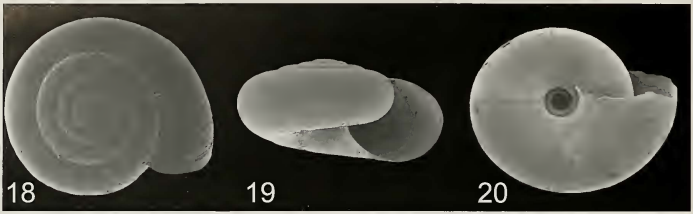
Pilsbryna nodopalma new species
Common name: oar tooth bud
(Figures 18–24, Table 1)

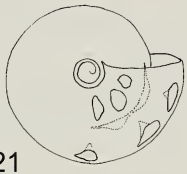
Pilsbryna (unidentified): Lee, 1990: 7–8, fig. (unnumbered)

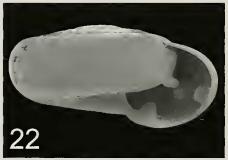
Diagnosis: A small and relatively loosely-coiled *Pilsbryna* of 2.7–3.2 mm diameter and 1.4–1.6 mm height, with 4.3–4.6 regularly expanding whorls. The shell whorls are widest above the middle. The shells of juvenile animals contain an undulate parietal lamella and three or four paired subcolumellar and lower palatal nodules grouped near the aperture. These nodules are dorsoventrally compressed.

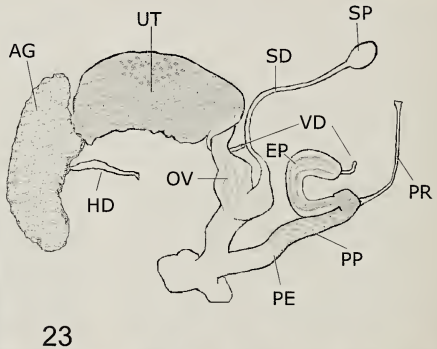
Description: The shell is depressed-helicoid, umbilicate and translucent. The shell is small and loosely coiled for the genus (Table 1); adults reach 2.7–3.2 mm (mean = 3.0, n = 10) greater diameter and 1.4–1.6 mm (mean = 1.5) height with 4.3–4.6 (mean = 4.5) whorls (Figures 18–20). Height is 0.47–0.53 (mean = 0.51) of the greater diameter. Whorl expansion is regular and increases only slightly in the last third of the body whorl; the ratio of lesser diameter to greater diameter is 0.83–0.90 (mean = 0.86). The shell surface is glossy and sculptured with weak and irregularly spaced indented axial lines. The apex is relatively flat and the whorls are widest slightly above mid-point. Spire width is 0.53–0.60 (mean = 0.58) of greater diameter. The sutures are relatively deeply impressed for the genus. The umbilicus is narrow, 0.4–0.5 mm (mean = 0.45) roughly 0.13–0.17 (mean = 0.15) of shell diameter. Juvenile shells, with less than four whorls, have an undulate parietal lamella and two to four, paired, subcolumellar and lower palatal nodules grouped near the aperture (Figures 21–22). These nodules are dorsoventrally compressed giving some of them the appearance of the tips of oar blades. The parietal lamella is undulate and is tallest where it passes the paired lower palatal and subcolumellar nodules. The distal edge of the parietal lamella points towards the lower palatal nodules.

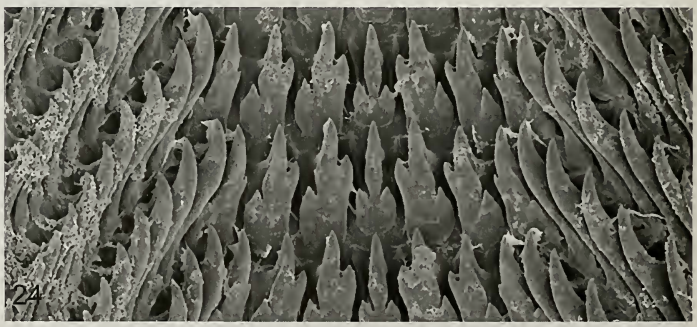
The penis is relatively short and moderately robust; it is apically papillate and basally smooth (Figure 23). The epiphallus is moderately short, about the same length and diameter as the penis. The penial retractor muscle is inserted nearly apically on the penis. The epiphallus is constricted slightly at the subapical junction with the penis and has strong internal longitudinal folds. The base of the spermathecal duct is robust with weak internal folds, the remainder of the duct is slender; the spermatheca is ovate. Interior of the vagina and free oviduct bear many folds. The free oviduct is roughly ⅓ larger than the base of the penis, expanding greatly at the junction with the spermathecal duct and narrowing again before the junction with the uterus. Description is based on two dissections.











Figures 18–24. *Pilsbryna nodopalma.* **18–20.** UF 294574, diameter 3.2 mm. **21.** UF 294574, diameter 3.2 mm; **22.** UF 24574. **23.** Camera lucida drawings of genitalia, UF 294575, maximum width 4.0 mm. **24.** UF 294575, horizontal field width 167 μm.

The central tooth of the radula is tricuspid; the mesocone is elongate (Figure 24). The ectocones are short, symmetric and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall and flare away from the mesocone, while the ectocones are short and not as strongly differentiated. The peripheral margin of the mesocone of the laterals is concave above the ectocone. There are twelve unicuspid marginal teeth on each side, all with concave peripheral and convex proximal, margins. Based on the examination of two radulae.

Holotype: UF 304986, J. Slapcinsky and H. G. Lee, 9 Jun. 2001.

Paratypes: UF 286492, type locality, B. A. Brown, May 1989; UF 294574, UF 294575, type locality, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 294573, UF 294574, Betsy's Gap, State Road 209, 0.5 km SW of summit, 35°41.3′ N, 82°54.3′ W, 1150 meters elevation; UF 294571, UF 294571, J. Slapcinsky, 11 Mar. 2001, 29 May 2001; UF 292056, Harmon Den Road 1.4 km SW of Max Patch Road, 35°46.5′ N, 82°57.8′ W, 1000 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 292713, Madison County: State Road 63 at Friezeland Creek, 35°43.6′ N, 82°50.5′ W, 1000 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2001; UF 294577, 0.3 km NE of junction of State Road 1175 and State Road 1182, 35°44.7′ N, 82°57.0′ W, 1170 meters elevation, J. Slapcinsky and H. G. Lee, 9 Jun. 2002; BC 1930, Tennessee, Greene County: Cherokee National Forest, Paint Creek Use Area, Hurricane Gap Road 3.2 km from Paint Creek, 35°57.9′ N, 82°50.5′ W, 640 meters elevation, B. Coles; UF 293022, Paint Creek near Forest Road 31, 1.3 km SW of fee station, 35°58.3′ N, 82°51.0′ W, 500 meters elevation, J. Slapcinsky, 1 Jun. 01; UF 293059, Paint Creek Road 5.3 km SW of fee station near junction with Forest Road 31, 35°57.3′ N, 82°53.4′ W, 420 meters elevation, J. Slapcinsky, 1 Jun. 01; BC 6763, Forest Road 3 by Paint Creek, B. Coles, 21 May 2002, 35°58.6′ N, 82°50.7′ W.

Type locality: USA, North Carolina, Haywood County, Carter Mountain Road at small stream 0.3 km SE of State Road 209, 35°40.7′ N, 82°54.4′ W, 1030 meters elevation.

Habitat and Distribution: *Pilsbryna nodopalma* is known from sites that extend for 50 km along the mountains on the North Carolina-Tennessee border, northwest of Asheville. Specimens have been found at 400–1100 m elevation usually on wooded, rocky hillsides in leaf-litter. Although, like other species of *Pilsbryna*, this species is found in moist leaf-litter, it is also found among leaves on relatively dry rock outcrops.

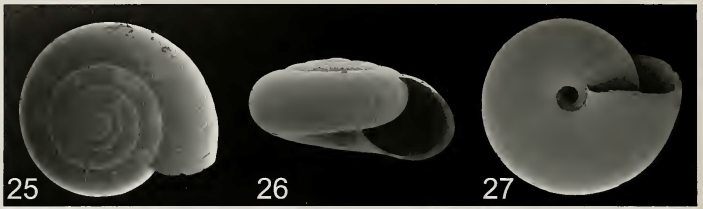
Etymology: Named for the dorsoventrally compressed apertural nodes that resemble the ends of oars (Latin, *noda* = knot and *palma* = palm or oar blade). For the purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988, 1998) and other administrative uses, the common name "oar tooth bud" is proposed.

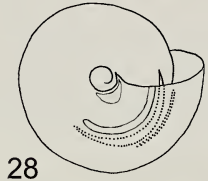
Remarks: Juveniles of *Pilsbryna nodopalma* are most likely to be confused with *P. vanattai*, the only other species with a series of palatal nodules. *Pilsbryna nodopalma* has nodules at the lower palatal position and the distal edge of the parietal lamella points toward these. In contrast, in *P. vanattai* the nodules are at midpalatal position and the distal edge of the parietal lamella points below these nodules. The nodules of *P. nodopalma* are dorsoventrally compressed, unlike the simple peg-shaped to elongate nodules of *P. vanattai*. Adults of *P. nodopalma* differ from all other species of *Pilsbryna* in having the whorls widest above mid-point rather than below. The penis, epiphallus and free oviduct are more robust than in other species of *Pilsbryna* except for *P. vanattai*. The endocones of the lateral teeth of *P. nodopalma* flare away from the mesocone, more so than any other species of *Pilsbryna*. A juvenile *Pilsbryna* specimen figured by Lee (1990) is this species.

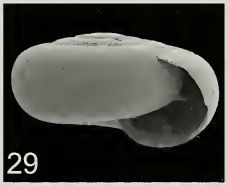
Pilsbryna quadrilamellata new species
Common name: four blade bud
(Figures 25–31, Table 1)

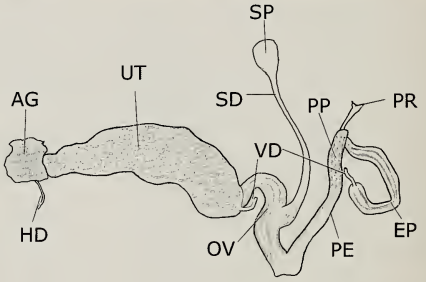
Diagnosis: A small to medium sized *Pilsbryna* with a shell of 2.8–3.2 mm diameter, 1.5–1.8 mm height, with 4.7–5.2 slowly expanding whorls. Shells of immature animals contain four lamellae, a crescent-shaped umbilical lamella and blade-shaped parietal, basal and sutural lamellae located within ⅓ whorl of the aperture. Lamellae are reduced in adult specimens; however traces of lamellae, especially the basal lamella are visible in the shells of many adults.

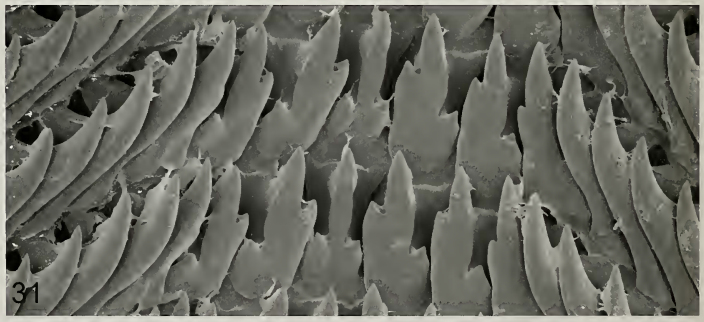
Description: Shell depressed-helicoid, umbilicate, glossy, and translucent with a sculpture of dense and irregularly spaced indented axial lines (Figures 25–27). Adult shells (Table 1) are about 2.8–3.4 mm (mean = 3.2, n = 10) in major diameter and 1.5–1.8 mm (mean = 1.7) in height with 4.7–5.2 (mean = 5.0) whorls. Shell height is 0.47–0.61 (mean = 0.52) of greater diameter. The whorls expand slowly and regularly; the lesser/greater diameter ratio of adult shells is 0.81–0.91 (mean = 0.87) the spire-width/greater diameter ratio 0.55–0.67 (mean = 0.61). The funnel-shaped umbilicus expands regularly; the umbilical width is 0.4–0.6 mm (mean = 0.5) and the ratio of umbilical width to greater diameter is 0.13–0.19 (mean = 0.17). The aperture of juvenile shells is evenly crescentic. In adults the sutural edge of the lip is flattened and the body whorl is widest basally. Shells of juveniles contain four lamellae at columellar, basal, sutural and parietal positions (Figures 28–29). The columellar lamella is short and crescent-shaped and is easily seen through the translucent base of the shell, although it often does not reach near enough to the aperture to be seen in apertural view. The basal lamella is thick, the distal edge broadly rounded. The sutural lamella is narrow, the distal edge evenly rounded and is











Figures 25–31. *Pilsbryna quadrilamellata*. **25–27.** UF 292445, diameter 3.4 mm. **28.** UF 292445, diameter 2.5. **29.** UF 292445, diameter 2.1 mm. **30.** Camera lucida drawings of genitalia, UF 292442, maximum width 5.8 mm. **31.** UF 292442, horizontal field width 150 μm.

most easily seen in an apical view through the translucent shell. The parietal lamella is thin and blade-shaped, tapering distally to a sharp edge. All four lamellae are reduced as individuals reach maturity; however some trace of lamellae, especially the basal lamella, remains in many adults.

The penis is relatively long and slender, apically papillate and basally smooth (Figure 30). The epiphallus is moderately long and slender, roughly the same diameter and length as the penis. The penial retractor muscle is inserted nearly apically on the penis. The epiphallus joins the penis subapically. The interior of the epiphallus bears strong internal folds. The spermathecal duct is long and slender and expands slightly at the junction with the free oviduct. The interior of the vagina, free oviduct and base of the spermathecal duct have weak folds. The free oviduct is about ⅓ larger than the base of the penis, and does not expand significantly at the junction with the base of the spermathecal duct. Two animals were dissected.

The central tooth of the radula is tricuspid; the mesocone is very slender and elongate (Figure 31). The ectocones are relatively short, a little more than ⅓ the total tooth height, symmetric and not significantly constricted basally. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall, while the ectocones short, less than ⅓ the height of the entire tooth. Both ectocones and endocones flare strongly away from the mesocone. Each side of the radula has eighteen, tall, slender and unicuspid marginal teeth, with concave peripheral and convex proximal margins. Description is based on examination of two radulae.

Holotype: UF 304987, J. Slapcinsky and B. Coles, 31 May 2001.

Paratypes: All from type locality: UF 292442, UF 292445, J. Slapcinsky and B. Coles, 31 May 2001; BC 6760, B. Coles, 20 May 2002; UF 288172, UF 297415, J. Slapcinsky, 10 Jun. 2002; UF 299538, J. Slapcinsky, 10 Sep. 2002.

Type Locality: USA, Tennessee, Unicoi County, Unaka Springs, cold air slope along Unaka Springs Road, 3.2 km S of Banner Hill, 36°05.9′ N, 82°26.7′ W, 520 meters elevation.

Habitat and Distribution: All *Pilsbryna quadrilamellata* specimens were collected from leaf-litter within approximately 20 m of the base of a talus slope on a NE facing slope of the Nolichucky River. The riverbank supports hemlock forest with cove hardwoods on thin, rich soil overlaying sandstone talus, with pockets of deep leaf-litter. A steady stream of cold air emanates from the base of the talus slope throughout the spring, summer, and fall. Local residents visit the cold air slope during the summer months and part of the base of the slope has been cleared to provide a seating area.

Etymology: Named for the unique arrangement of four blade-like apertural barriers (Latin, *quattuor* = four and *lamella* = blade). For the purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988, 1998) and other administrative uses, the common name "four blade bud" is proposed.

Remarks: The juvenile shell of *P. quadrilamellata* is unique in having a sutural lamella and a basal lamella that is long, thick and evenly rounded distally. It is most similar to *P. aurea*, both species having a crescent-shaped columellar lamella. The body whorl of *P. quadrilamellata* does not expand rapidly at maturity like most other *Pilsbryna* species. Adult *P. quadrilamellata* are unusual in having the sutural margin of the final third of the body whorl flattened. The penis and epiphallus of *P. quadrilamellata* are unusually delicate and elongate. The penis and epiphallus are uniform in width throughout, similar only to *P. nodopalma* and *P. vanattai*. The endocones of the lateral teeth of the radula flare strongly, similar only to those of *P. nodopalma* and the ectocones are relatively shorter than in any other species of *Pilsbryna*.

Pilsbryna vanattai (Walker and Pilsbry, 1902) new combination

Common name: honey glyph

(Figures 32–38, Table 1)

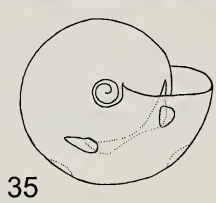
Vitrea vanattai Walker and Pilsbry, 1902: 432, pl. 23, figs. 4–6

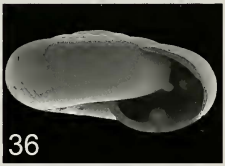
Retinella (*Glyphyalus*) *vanattai* (Walker and Pilsbry, 1902). Baker, 1930: 205, pl. 10, figs. 9, 10; Pilsbry, 1946: 273–274, Fig 135; Burch 1962: 98, fig. 229.

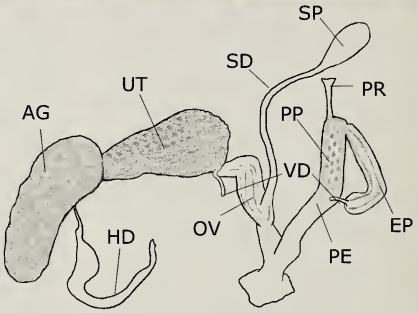
Glyphyalinia vanattai (Walker and Pilsbry, 1902). Baker, 1962: 20; Hubricht, 1970: 13; Hubricht, 1985: 23, Map 212; Turgeon et al., 1988: 134; Turgeon et al., 1998: 147.

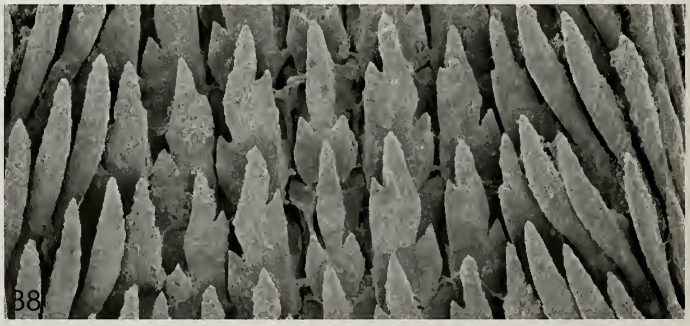
Diagnosis: A medium to large-sized, relatively depressed and loosely coiled *Pilsbryna* with a shell of 3.8–4.4 mm diameter and 1.9–2.2 mm height with 4.6–5.1 whorls. The body whorl of adults expands rapidly; the ratio of greater/lesser diameter of adult shells is 0.80–0.89. Juveniles have a sinuous parietal lamella and two spirally arranged series of one to three widely spaced paired basal and palatal nodules. The palatal lamella occupies a position lateral to and slightly above the parietal nodules.

Description: Shell depressed-helicoid, umbilicate, and fragile, sculptured with irregular, impressed, axial lines (Figures 32–34). The sutures are shallow. Adult shells are relatively large (Table 1), 3.8–4.4 mm (mean = 4.0, n = 10) diameter, and 1.9–2.2 mm (mean = 2.0) height with 4.6–5.1 (mean = 4.8) whorls. The whorls expand slowly and regularly up to four whorls and then very rapidly, the ratio of lesser/greater diameter of adult shells is 0.80–0.89 (mean = 0.84). The rapid expansion of the body whorl results in low ratios for shell height/greater diameter of 0.48–0.56 (mean = 0.51) spire width/greater diameter 0.48–0.56 (mean 0.52) and umbilical width/greater diameter of 0.12–0.16 (mean = 0.14). The umbilicus is narrow until the final third of the









Figures 32–38. *Pilsbryna vanattai.* **32–34.** UF 279916, diameter 4.0 mm. **35–36.** UF 279916, diameter 2.0 mm. **37.** Camera lucida drawings of genitalia, UF 279917, maximum width 5.7 mm. **38.** UF 279917, horizontal field width 160 μm.

body whorl and then expands rapidly to 0.5–0.6 mm (mean = 0.5). Immature shells with fewer than 3.5 whorls have three lamellae: a sinuous parietal lamella and a series of paired basal and palatal nodules. When viewed from the aperture, the palatal lamella is situated lateral to and slightly above the parietal lamella. Two to three pairs of palatal and basal nodules can usually be seen through the base of the juvenile shell (Figures 35–36). These barriers are widely spaced, up to ⅓ whorl apart, and are usually completely resorbed in shells over 4 whorls. The undulating parietal lamella extends up to ⅔ of a whorl and is more prominent where it passes the paired basal and palatal lamellae.

The penis is papillate on its apical third and smooth basally (Figure 37). The penial retractor muscle inserts apically on the penis. The epiphallus joins the penis laterally at the apex, is short, only ⅔ the length of the penis, and robust, slightly narrower than the penis. The epiphallus is folded near mid-point, its interior has several strong, longitudinal folds and it is slightly swollen at the junction with the vas deferens. The interior of the vagina, free oviduct, and base of the spermathecal duct, bear many longitudinal folds. Three animals were dissected.

The central tooth of the radula is tall, slender and tricuspid (Figure 38). The mesocone is elongate, widest near mid-point and tapers apically and narrows basally. The ectocones are short, symmetrical and diamond-shaped. The three lateral teeth are tall, slender and asymmetrically tricuspid. The endocones of the laterals are tall and the ectocones short. The ectocones and endocones are well defined, but do not flare strongly away from the mesocone. The peripheral edges of the first two lateral teeth are concave. The third lateral tooth is notched above the ectocone. The twenty-two marginal teeth on each side of the radula are tall, slender and unicuspid, with concave peripheral edges and convex proximal edges. Two radulae were examined.

Lectotype: ANSP 83261a.

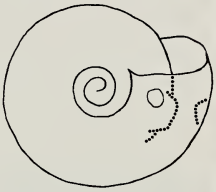
Paralectotype: ANSP 410030, from type locality, J.H. Ferriss, 1901.

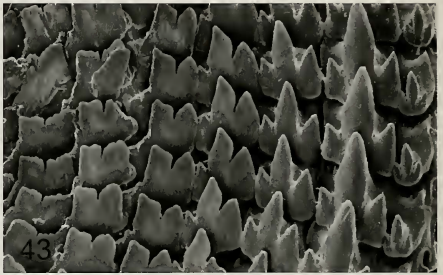
Type Locality: USA, North Carolina, Yancey County, Mount Mitchell, J. H. Ferriss, 1901.

Other Material Examined: USA, North Carolina: Avery County, Cranberry, Baker (ANSP 158889). Buncombe County: Pisgah National Forest: State Road 197 ca. 9 km E of Barnardsville, 35°47.9′ N, 82°22.1′ W, 985 m elevation, J. Slapcinsky, 29 Apr 2000 (UF 279987); Walker Cove, Forest Road 74, ca. 7 km E of Dillingham, 35°45.7′ N, 82°21.6′ W, 1140 m elevation, J. Slapcinsky and R. Caldwell, 24 Apr 1998 (UF 279967), J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279916, UF 279917), J. Slapcinsky, 13 Mar 2001 (UF 287012), J. Slapcinsky, 1 Jun 2001 (UF 287010, UF 287011); Forest Road 74 at Perkins Road Trail, 35°44.9′ N, 82°21.4′ W, 1200 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279983, UF 279984); Forest Road 74, 0.5 km N of Laurel Gap Trail, 35°44.5′ N, 82°21.9′ W, 1200 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279986, NCSM P-4731); Douglas Falls Trail, 0.5 km S of Forest Road 74, 35°43.2′ N, 82°22.4′ W, 1350 m elevation, J. Slapcinsky and S. Florence, 27 Apr 2000 (UF 279988); Forest Road 63 ca. 8 km S of Dillingham, 35°42.6′ N, 82°23.7′ W, 1190 m elevation, J. Slapcinsky, 2 Jun 2001 (UF 287013); Bent Creek Experimental Forest, Forest Road 479, ca 1 km N of Blue Ridge Parkway, 35°27.7′ N, 82°39.7′ W, 860 m elevation, J. Slapcinsky, 2 Jun 2001 (UF 288621, UF 288622). Mitchell County: 1.9 km E of Spruce Pine, L. Hubricht, 4 Jun 1964 (FMNH 240499); Magnetic City, A. G. Wetherby, 1893 (ANSP 64609). Yancey County: near South Toe River, 7.2 km E of Mount Mitchell, 975 m elevation, L. Hubricht, 26 May 1962 (FMNH 240500); Black Mountains, Cat Tail Cove, J. H. Ferriss, 1901 (ANSP 84066). Tennessee: Carter County: Iron Mountain, Forest Road 4331 at Fall Branch, 36°9.1′ N, 82°10.7′ W, 1180 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292523); Roan Mountain, State Road 143 at Dave Miller Hollow Road, 36°10.3′ N, 82°6.1′ W, 840 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292505); Roan Mountain, behind picnic area W of Dave Miller Hollow Road, 36°10.3′ N, 82°5.9′ W, 850 m elevation, J. Slapcinsky and B. Coles, 30 May 2001 (UF 292470); 4.0 km S of Roan Mountain, L. Hubricht, 21 Sep 1967 (FMNH 240502); N outliers of Roan Mountain, Baker (ANSP 158887). Unicoi County, State Road 107, 0.5 km E of Red Fork Road, 36°9.2′ N, 82°14.9′ W, 880 m elevation, J. Slapcinsky and B. Coles, 31 May 2001 (UF 293083).

Habitat and Distribution: *Pilsbryna vanattai* has been found at sites between 800 and 1400 m elevation, ranging 120 km along the Blue Ridge of North Carolina and W into extreme eastern Tennessee (Pilsbry, 1946; Hubricht 1970, 1985). Specimens located in this survey were found at the soil leaf-litter interface on rich wet soils within a few meters of seeps, springs and small streams, often among stinging nettles, *Laportea canadensis* (Linnaeus, 1753), but also, less commonly, in deep leaf-litter at the base of rock outcrops.

Remarks: The juvenile shell of *Pilsbryna vanattai* differs from that of *P. nodopalma*, the only other species with palatal nodules, in having nodules that are not dorsoventrally compressed and that are located at mid-palatal rather than sub-palatal position. The body whorl of *P. vanattai* expands more rapidly than any other species of *Pilsbryna*. *P. vannattai* has the lowest ratios of lesser diameter/greater diameter, height/greater diameter, spire width/greater diameter, and umbilical width/greater diameter of any *Pilsbryna* species. The penises of *P. vanattai* and *P. nodopalma* are more robust than those of other species of *Pilsbryna*. The epiphallus of *P. vanattai* is relatively shorter than any other species, only about ⅔ the length of the penis. The ectocones and endocones of the lateral teeth of *P. vanattai* are well differentiated, unlike *P. aurea* and *P. castanea*, but do not





Figures 39–43. *Helicodiscus tridens.* **39–41.** UF 286491, diameter 1.6 mm. **42.** UF 286491, diameter 1.4 mm. **43.** UF 286491, horizontal field width 42 μm.

flare away from the mesocone, unlike *P. nodopalma* and *P. quadrilamellata.*

Walker and Pilsbry (1902) did not designate a holotype for *P. vanattai.* A single set of approximate measurements was given, but these could refer to either of the two adults of the three specimens mentioned in the description. Baker (1962) selected the specimen figured by Walker and Pilsbry (1902, figs. 4–6) to be the 'type', thereby designating the lectotype, and segregated it as 83261a. The remainder of the lot, the two paralectotypes, remained ANSP 83261. Later, the juvenile paralectotype was lost and the remaining paralectotype was recataloged (ANSP 410030).

Family Helicodiscidae
Genus *Helicodiscus* Morse, 1864

Helicodiscus tridens (Morrison, 1935)
Common name: crosstimbers coil
(Figures 39–43)

Pilsbryna tridens Morrison, 1935: 546, figs. 8–10; Pilsbry, 1946: 393, fig. 209; Burch, 1962: 106 fig. 25; Cheatum and Fullington, 1971: 9, fig. 12.

Helicodiscus tridens (Morrison, 1935). Hubricht, 1964: 28; Riedel, 1980: 52; Hubricht 1985: 20, fig. 182; Turgeon et al., 1988: 131; Turgeon et al., 1998: 148.

Holotype: USNM 359722, P. V. Roundy.

Type Locality: USA, Texas, Palo Pinto County, near Strawn.

Other Material Examined: USA, Oklahoma: Muskogee County, South Canadian River at Highway 2, 35°15.8′ N, 95°14.4′ W, 150 m elevation, B. Coles, 28 Nov 1998 (UF 286491); Haskell County, South Canadian River, Whitefield, L. Hubricht, 1935 (FMNH 239114); Texas, Colorado County, Colorado River at Columbus, H. F. Wickham, 8 Jan 1953 (ANSP 189563).

Habitat and Distribution: All previously known specimens of *Helicodiscus tridens* were collected from river drift or Pleistocene deposits from central Oklahoma to central Texas (Hubricht, 1985). Recent specimens of *H. tridens* including one with a dried animal were sifted from leaf-litter under willows, *Salix* sp.

Remarks: Comparisons of the species described in the genus *Pilsbryna* have highlighted the need to resolve the generic placement of *Helicodiscus tridens* (Morrison, 1935). *Helicodiscus tridens* was described as a *Pilsbryna* species based on similarities in the apertural barriers. Hubricht (1964) moved the species to the genus *Helicodiscus.* However, the basis for this change was not given, and the generic placement of the species has re-

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Figure 44. Distribution of *Pilsbryna*: a = *Pilsbryna aurea*, c = *P. castanea*, n = *P. nodopalma*, q = *P. quadrilamellata*, v = *P. vanattai*. Map scale: 1 cm = 18 km.

mained unresolved. Characters other than those of the shell previously have not been available for study. Newly collected material, including a single dried animal, allows comparisons of both shell and radular morphology among *H. tridens* and species of *Pilsbryna* and *Helicodiscus*. Characters of the shell (Figures 39–42), including the nearly circular aperture, the small number of whorls (about 4 in adults), the flat apex and base, the impressed sutures, and the regularly expanding umbilicus, are not similar to species of *Pilsbryna*. However, they are consistent with *Helicodiscus, sensu lato*. The radula of *H. tridens* differs from *Pilsbryna* species. The row of tiny central teeth (Figure 43, far right), the much larger symmetric tricuspid lateral teeth and the short, broad, multicuspid marginal teeth are characteristic (Solem, 1975) of the helicodiscidae but are not found in *Pilsbryna*, thereby supporting Hubricht's (1964) placement of *H. tridens* in *Helicodiscus*.

DISCUSSION

When species of *Paravitrea* and *Helicodiscus* are separated from *Pilsbryna*, the geographic and microhabitat distribution of *Pilsbryna* is clarified. All known populations of *Pilsbryna* occur near springs, seeps and mountain streams in the southern Appalachian Mountains and nearby Cumberland Plateau (Figure 44). Within these areas, *Pilsbryna* species occupy moist microhabitats in damp, often deep, leaf-litter. It is likely that *Pilsbryna* species would be intolerant of habitat changes affecting

soil hydrology and leaf-litter cover. The narrow distribution and habitat specificity of species of *Pilsbryna* should make them species of special concern to land managers.

The terrestrial molluscan fauna of the southern Appalachian Mountains is by far the most diverse in eastern North America (Hubricht, 1985). Diversity notwithstanding, the region is still not well sampled, especially for small species with narrow habitat requirements. Recent collecting efforts in wet leaf-litter microhabitats uncovered not only the species reported here but also several others that require additional material to adequately describe. These results suggest there is a largely unreported radiation of *Pilsbryna* at springs and seeps throughout the southern Appalachian Mountains and Cumberland Plateau. Additional collecting in this region is necessary to determine the scope of this radiation.

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LITERATURE CITED

Baker, H. B. 1929a. New southern Appalachian land snails. The Nautilus 42: 86–93.

Baker, H. B. 1929b. Psendohyaline American land snails. Proceedings of the Academy of Natural Sciences of Philadelphia 81: 251–266.

Baker, H. B. 1930. The North American retinellae. Proceedings of the Academy of Natural Sciences of Philadelphia 82: 193–219.

Baker, H. B. 1931. Nearctic vitreine land snails. Proceedings of the Academy of Natural Sciences of Philadelphia 83: 85–117.

Baker, H. B. 1962. Type land snails in the Academy of Natural Sciences of Philadelphia I. North America, North of Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 114: 1–21.

Burch, J. B. 1962. How to know the eastern land snails. Wm. C. Brown, Dubuque. 214 pp.

Cheatum, E. P. and R. W. Fullington. 1971. Keys to the families of the recent land and fresh-water snails of Texas. Dallas Museum of Natural History, Bulletin 1(supplement): 1–18.

Emberton, K. C. 1985. Seasonal changes in the reproductive gross anatomy of the land snail *Triodopsis tridentata tridentata* (Pulmonata: Polygyridae). Malacologia 26: 225–239.

Hubricht, L. 1964. *Helicodiscus tridens* and *Helicodiscus aldrichiana.* The Nautilus 78: 28.

Hubricht, L. 1970. The land snails of North Carolina. Sterkiana 39: 11–15.

Hubricht, L. 1973. The land snails of Tennessee. Sterkiana 49: 11–17.

Hubricht, L. 1985. The distribution of the native land mollusks of the eastern United States. Fieldiana, Zoology, New Series 24: 1–191.

Lee, H. G. 1990. Toward an improved strategy for landsnail collecting. The Shell-O-Gram 31(1): 3, 6–8.

Morrison, J. P. E. 1935. Three new land shells from the southern United States. Journal of the Washington Academy of Sciences 25(12): 545–547.

Pilsbry, H. A. 1946. Land Mollusca of North America (north of Mexico), The Academy of Natural Sciences of Philadelphia, Monograph 3, 2(1): 1–520.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico), The Academy of Natural Sciences of Philadelphia, Monograph 3, 2(2): 521–1113.

Riedel, A. 1980. Genera zonitidarum diagnosen supraspezifischer taxa der familie Zonitidae (Gastropoda, Stylommatophora). Dr. W. Backhuys, Rotterdam. 197 pp.

Solem, A. 1975. *Polygyriscus virginianus* (Burch, 1947) a helicodiscid land snail (Pulmonata: Helicodiscidae). The Nautilus 89(3): 80–86.

Tompa, A. S. 1984. Land snails (Stylommatophora). In A. S. Tompa, N. H. Verdonk and J. A. M van den Biggelaar (eds.), The Mollusca, Volume 7, Reproduction. Academic Press: New York, pp. 47–140.

Turgeon, D. D., A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson and J. D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. American Fisheries Society Special Publication 16, 277 pp.

Turgeon, D. D., J. F. Quinn, Jr., A. E. Bogan, E. V. Coan, F. G. Hochburg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione and J. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, second edition. American Fisheries Society Special Publication 26, 526 pp.

Walker, B. and H. A. Pilsbry. 1902. The Mollusca of the Mt. Mitchell region, North Carolina. The Proceedings of the Academy of Natural Sciences of Philadelphia 54: 413–442.